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Wisdom of the crowd: evidence for density-dependent species fitness in *Hyptis suaveolens* (L.) Poit.

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Abstract

Background Biological invasions pose severe threats to global biodiversity and human well-being. Invading populations often experience negative growth rates during the 'lag phase', leading to Allee effects, a density-dependent phenomenon. Allee effects reduce species fitness or plant performance due to low-density populations. The rapid spread and range expansion of an invader, *Hyptis suaveolens* (L.) Poit. has been reported to have negative impacts on local biodiversity in the invaded regions of the Vindhyan highlands, India. The present study examines the effects of varied population densities of *H. suaveolens* on its vegetative trait performance, reproductive output, and density-dependent plant population regulations. Understanding the relationship between the population density and trait modulation ability of *H. suaveolens* at fine and coarse scales could help strategize for management.

Methods The study was conducted in invaded habitats of *H. suaveolens* in the Vindhyan highlands, India. Population density was divided into low-, medium-, and high-density groups. Plant performance was assessed at two scales—fine scale and coarse scale. Plant performance traits, vegetative growth, and reproductive output were estimated as plant traits (PITs) at the fine scale and patch traits (PaTs) at the coarse scale. The plasticity response index (PI) was also estimated among three population densities.

Results Results showed that PITs-vegetative and reproductive traits, such as plant height, biomass, and number of seeds, were significantly different across densities, with medium-density individuals showing maximum plant height and plant biomass and high-density individuals exhibiting a higher number of seeds per plant. PaTs analysis revealed that plant biomass per patch was similar for medium- and high-density populations, whereas the number of seeds per patch was similar in low- and medium-density populations. PI values revealed that PITs showed low, medium, and high plastic responses, while PaTs exhibited low and high plastic responses.

Conclusions The study concludes that *H. suaveolens* exhibits density-dependent plant population regulations. As population density increases, low-density populations grow more rapidly, resulting in denser populations. These populations can negatively impact recipient habitats and, if left unchecked, grow into high-density populations with higher seed production. The study suggests that low-density areas should be considered a high priority for developing efficient and cost-effective management strategies. The present study emphasizes the importance of incorporating Allee effects dynamics in invasion studies for predicting high-risk/priority areas for strategizing invasive species management.

Keywords Allee effect, Lag phase, Population density, Plastic response, Elastic response, Fine scale, Coarse scale, Plant performance trait

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Introduction

Biological invasions cause severe consequences for global biodiversity and human well-being (Courchamp et al. 2017; Lenzner et al. 2020; Bellard et al. 2022; Bargali 2024). The detrimental effects of invasive plant species are often associated with their large and dense populations (Khatri et al. 2024a, b; Negi et al. 2025). Primarily, most biological invasion studies have focused on the establishment and range expansion of these large populations. However, introduced/founding populations are often small-sized with low density. These founding populations potentially facilitate novel impending introduction incidents to non-native areas, establishment of introduced populations, and range expansion of introduced and/or existing invasive populations (Dawson et al. 2008; Ross and Shoemaker 2008). During the establishment phase, plant species with high invader potential show efficient growth and reproduction strategies leading to self-sustaining populations (Goyal et al. 2018; Shah et al. 2024). Range expansion is a crucial phase since not all colonizing species become widespread at once (Williamson and Fitter 1996; Keitt et al. 2001; Sakai et al. 2001; Excoffier et al. 2009; Gioria et al. 2023). However, the failure of introductions is poorly understood.

In general, invasion success has been linked to intrinsic as well as extrinsic traits in novel environments (Dey et al. 2019; Khatri et al. 2022; Negi et al. 2025). Intrinsic traits encompass life history or morpho-functional traits, such as high growth rates, high biomass generation, rapid reproduction, ability to disperse, plasticity, and allelopathy (Hamilton et al. 2005; Ni et al. 2021; Negi et al. 2023a; Khatri et al. 2024a). Extrinsic traits refer to the environmental characteristics of the invaded habitats, such as topography and biological diversity, and characteristics of the interacting native vegetation, such as resource availability, lack of natural enemies, and disturbance levels (Wavrek et al. 2017; Lannes et al. 2020; Khatri et al. 2023). Disturbance is considered one of the important extrinsic traits of a habitat's susceptibility to invasion (Negi et al. 2024).

In most of the cases, colonizing populations often undergo a 'dormant' or 'lag' phase—a period of slow population growth rate and delayed range expansion that is followed by a phase of rapid population explosions and spread of invading populations (Simberloff 2003; Aikio et al. 2010; van Klinken et al. 2015; Holden et al. 2016). Consequently, owing to the low population density, founding populations could be subjected to Allee effects, a density-dependent phenomenon (Tobin et al. 2011). Allee effects dynamics are characterized by reduced species fitness or reductions in components of species fitness (plant performance traits) in response to a decrease in population density (Allee 1931; Stephens et al. 1999).

Essentially, Stephens et al. (1999) described Allee effects as "positive relationships between component(s) of individual fitness and either numbers or density of conspecifics." Numerous studies have addressed the ubiquity of Allee effects among major animal taxa such as Arthropoda, Chordata, Mollusca, and Vertebrates (Shah and Sharma 2022). However, the need for research on Allee effects is an absolute necessity for invasive plants, as plant invaders have been given far less attention than animal invaders (Kramer et al. 2009; also see Shah 2024). In turn, Allee effects may also provide a unique opportunity to learn about the possible explanation for the 'lag' phase during the early stages of species invasion.

Adverse impacts on the local biodiversity, ecosystem services, and environmental quality are further exacerbated by the rapid spread and range expansion of invasive plants: grass species such as *Arundo donax* L. (Plaza et al. 2018), *Bromus tectorum* L. (Morris et al. 2016), *Parthenium hysterophorus* L. (Cai et al. 2016), and *Solidago gigantea* Aiton (Stefanowicz et al. 2018); herbaceous species such as *Ageratina adenophora* (Spreng.) R.M. King & H. Rob. (Negi et al. 2023b; Khatri et al. 2024a, b), *Hyptis suaveolens* (L.) Poit. (Shah et al. 2024), *Impatiens glandulifera* Royle (Gaggini et al. 2018), and *Reynoutria japonica* Houtt. (Rouified et al. 2012); shrub species such as *Chromolaena odorata* (L.) R.M. King & H. Rob. (Shrestha et al. 2018), *Lantana camara* L. (Goyal and Sharma 2019), and *Mikania micrantha* Kunth (Guo et al. 2018); and tree species such as *Ailanthus altissima* (Mill.) Swingle (Planchuelo et al. 2016), *Chamaecyparis lawsoniana* (A. Murray bis) Parl. (Green et al. 2013), and *Phellodendron amurense* Rupr. (Morgan and Borysiewicz 2012). Among the fast-spreading invasive species, *H. suaveolens* is an important invader of the tropical and subtropical regions around the world (CABI 2024). Native to tropical America, *H. suaveolens* has spread widely across the world and in tropical Africa, Asia, and Australia (CABI 2024). In India, British botanist Joseph Dalton Hooker recorded its occurrence in the late nineteenth century in the Deccan and Cachar regions but not in north India (CABI 2024). In the late 1900s, researchers reported innocuous, naturalized infestations of *H. suaveolens* sparse and less dense populations in the foothills and edges of open forest in India (Verma and Mishra 1992; Mudgal et al. 1997).

Researchers suggested the occurrence of density-dependence in the invasive populations of *H. suaveolens*, a dominant plant invader, in the dry deciduous regions of the Vindhyan highlands, India (Sharma and Raghubanshi 2009; Sharma et al. 2009). In recent years, heavy infestations of *H. suaveolens* have been reported in the interior forest openings and forest clearings in the Vindhyan highlands (Afreen et al. 2018, 2020; Shah et al.

2024). In India, dense monospecific thickets of *H. suaveolens* are commonly found in degraded open forest areas, wastelands, along railway lines, and on road verges. *H. suaveolens* shows trait modulation ability and can thrive and proliferate across a wide range of environmental conditions (Raizada 2006; Shah 2024; Shah et al. 2024). Invasion success of *H. suaveolens* has been attributed to strategic trait modulations/plastic response to dynamic environmental conditions in non-native ranges (Sharma et al. 2009; Shah et al. 2024).

In general, invaded habitats are characterized by a mosaic of spatially segregated small and local populations (population patches) of introduced species during the initial stages of the invasion process. The spatio-temporal distribution of patches of varying population densities and sizes may be quite dynamic throughout the invasion process (Chabrerie et al. 2007). Associated changes in patch dynamics (establishment, growth, and local spread) in response to changes in population densities depend on plastic responses/trait modulations of plant performance traits that determine the growth and expansion of an invasive species (Eppinga et al. 2021). Plastic response is the ability (an intrinsic attribute) of a species to modulate its trait performance in response to a range of environmental conditions (van Kleunen and Johnson 2007; Flores-Moreno and Moles 2013; Khatri et al. 2024a). Plastic responses/trait modulations significantly increase the adaptation and range extension of a species in recipient environments (Leishman et al. 2000; Sharma and Esler 2008; Shah et al. 2024). It is anticipated that studying the relationship between the plastic responses/trait modulation ability of an invasive species and the patch dynamics (establishment, growth, and local spread) of variable population densities could play an important role in understanding the Allee effects dynamics and subsequently be utilized to strategize management.

Allee effects in plant invaders have either been assessed only on the reproductive success of mature individuals (Lamont et al. 1993; Groom 1998; Taylor and Hastings 2005; Tobin et al. 2011; Shah and Sharma 2022) or focused on already occurring populations exhibiting patchy distributions in the invaded habitats (Groom 1998; Hackney and McGraw 2001; Mavraganis and Eckert 2001; Taylor and Hastings 2005; Hui and Richardson 2017). However, substantiating a decrease in plant reproduction at low density does not necessarily prove the presence of Allee effects in the population. Populations exhibiting an Allee effect should have an optimal population density for invasion success; however, non-native species exhibiting sub-optimal population densities undergo invasion failure. Thus, Allee effects may restrict the establishment and colonization of invading populations (Taylor and Hastings 2005; Tobin et al. 2011; Shah

and Sharma 2022). To truly establish the occurrence of Allee effects, researchers must consider the effect of population density not just on reproduction but also on growth across varying population densities. In general, invasive species undergoing Allee effects either go extinct or overcome the deleterious effects to form a self-sustaining invasive population in due course of time. Therefore, it is necessary to understand and disentangle the relation between plant trait modulations and varying population densities.

The invasion process—introduction, establishment, and spread of introduced species—is highly complex and depends on a multitude of species functional traits. In addition to the ways in which these different traits contribute to biological invasions, their relative importance also varies at which spatial scales they are measured—fine scale and coarse scale (Parker et al. 1999; Ricklefs and Jenkins 2011). Identifying a suite of plant traits that an invader might possess signifies the fine scale (plant traits) (Xu et al. 2004; Michelan et al. 2013), and identification of plant traits responsible for invasive population success signifies the coarse scale (patch traits) (Stohlgren et al. 2006; Capers et al. 2007). At the fine scale (plant traits), the effects of plant functional traits are expected to be the most prevalent, whereas at the coarse scale (patch traits), demographic factors such as population density play an important role. In general, the majority of empirical studies on the determinant factors of plant invasions have focused only on a single scale (see Kotowska et al. 2024).

Founder populations, encountering the Allee effects, experience a substantial reduction in one or more fitness components (or plant traits) that manifest into a ‘component Allee effect’ at the fine scale. Consequently, a ‘demographic Allee effect’ is observed in population patches (or patch traits) at the coarse scale. Further, the component Allee effect may scale up to the demographic Allee effect. The occurrence of the demographic Allee effect in a founder population leads to a decline in per capita population growth rates or extinction in sparsely spaced populations (Taylor and Hastings 2005; Courchamp et al. 2008; Tobin et al. 2011; Hui and Richardson 2017). The occurrence of a demographic Allee effect, however, does not explain the underlying mechanism. To understand the mechanism of the demographic Allee effect, researchers need to investigate the component Allee effect (Stenglein and Van Deelen 2016; Hui and Richardson 2017). Understanding the component Allee effect may aid in the identification of possible mechanisms driving the density-dependent population dynamics in recipient habitats (Berec et al. 2007; Tobin et al. 2011; Kanarek et al. 2013). Additionally, knowledge of the demographic Allee effect can facilitate an informed risk assessment and potential

mitigation measures for early non-native introduction and establishment incidences.

Previous studies have reported the lack of empirical evidence (field studies and experiments) documenting the occurrence of the Allee effects in plant invaders (Boukal and Berec 2002; Courchamp et al. 2008; Shah and Sharma 2022). As much of the understanding of the impact of Allee effects on invasion success is derived from theoretical research and mathematical models (Shah and Sharma 2022). However, theoretical studies and mathematical models have demonstrated that incorporating Allee effects into biological invasion research can greatly enhance the ability to predict and manage invasions (Drake and Lodge 2006; Tobin et al. 2011; Shah and Sharma 2022). For example, Dennis (2002) studied a general stochastic population model that accounts for both demographic and environmental stochastic fluctuations to understand the deterministic and stochastic drivers in ecological populations. Guo and Chen (2010) investigated three mathematical models on the different management strategies of a single species exhibiting Allee effects. Murphy and Johnson (2015) presented a new individual-based, spatially explicit model to explore the role of Allee effects in the growth and population dynamics of *Spartina* spp. under specific local environmental conditions. Angulo et al. (2018) developed a mathematical model to investigate the effects of group size heterogeneity and intergroup interactions on the occurrence of the demographic Allee effect.

Varying population densities cause alterations in the environmental resources and create fluctuations in the degree of available space needed for invasive spread on a spatio-temporal scale. Thus, to understand the effect of population density on the establishment, proliferation, and spread of an invasive species, it is vital to study key performance-related plant traits that facilitate plant fitness across the life cycle of invasive species. In this context, Shah et al. (2024) emphasized that management of dense mono-specific thickets of *H. suaveolens* should be the utmost priority for the restoration and conservation of the degraded ecosystem of the Vindhyan highlands, India. Building on this, the current study hypothesizes that low population density may reduce vegetative growth and reproductive output of *H. suaveolens* individuals, indicating the occurrence of the 'component' Allee effect at fine scale (individual plant traits). At coarse scale (patch traits), population patches with sub-optimal densities may experience poor establishment and growth, leading to the 'demographic' Allee effect. However, patches exhibiting higher densities may overcome the deleterious impacts of the 'demographic' Allee effect due to species' trait modulation ability. Therefore, it is anticipated that the trait modulation ability of *H. suaveolens* in response

to varying population densities will play a crucial role in the invasion success and spread of *H. suaveolens* in the Vindhyan highlands. It is noteworthy that the present study is one of very few studies that incorporate the assessment of trait performance at both fine and coarse scales to investigate the occurrence of the Allee effects in invasive populations. With this understanding, the current study intends to specifically examine (i) whether population density affects the plant fitness, in terms of vegetative trait performance and reproductive output, of *H. suaveolens* individuals at fine scale (plant traits); (ii) whether population density affects the *H. suaveolens* plant fitness in terms of vegetative trait performance and reproductive output at coarse scale (patch traits); and (iii) how density-dependent plant population regulation facilitates *H. suaveolens* invasion success in the invaded regions of the Vindhyan highlands, India. Understanding how vegetative fitness and reproductive success vary with population density is key to assessing risks and managing invasive populations of *H. suaveolens*.

Materials and methods

Study site

The study was conducted in the dry deciduous forest of the Vindhyan highlands in the Sonbhadra district of Uttar Pradesh, India (23°52–25°32' N; 82°07–83°33' E). A reconnaissance survey showed that the study area is heavily infested with monospecific thickets of *Hyptis suaveolens*. The first reported occurrence of *H. suaveolens* in the intact forests of the Vindhyan highlands was documented by Agrawal (2002). Sharma and Raghubanshi (2009) reported the heavy infestations of *H. suaveolens* monospecific thickets in interior forest openings of the Vindhyan highlands. Recent studies investigated the effect of invasive populations of *H. suaveolens* on plant diversity in the study plots in the Vindhyan highlands in Uttar Pradesh (Afreen et al. 2018, 2020). Rahaman et al. (2022) reported that potentially ~88% of the tropical dry deciduous forest and non-forested regions of Jharkhand (a neighboring state that also comes under the Vindhyan ranges) is susceptible to the colonization of *H. suaveolens*. Shah et al. (2024) reported the occurrence of dense monospecific thickets of *H. suaveolens* in the dry deciduous forest of the Vindhyan highlands. *H. suaveolens* showed heavy infestations, with importance value indices (IVI) of ~72, in the dry deciduous forest of the Vindhyan highlands (Shah 2024). IVI signifies the relative measure of density, dominance, and abundance of one particular species among the other resident species in an area (Curtis 1959).

The study area is characterized by tropical monsoons with distinct hot and dry summers (March–June), warm

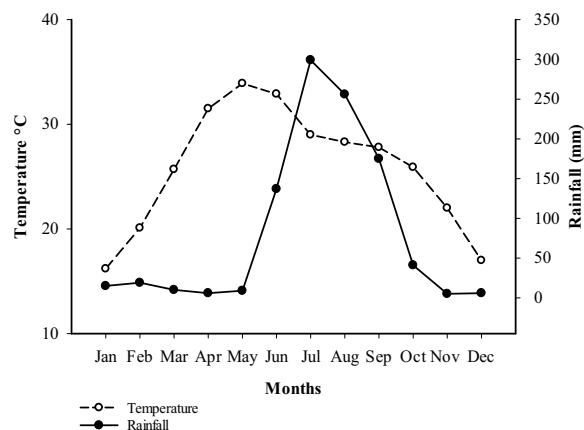


Fig. 1 Monthly average temperature (°C) and rainfall (mm) of the study area

and humid rainy seasons (July–October), and cold and dry winters (November–February) (Fig. 1). The mean annual temperature is ~25 °C with variable summer (20–34 °C) and winter temperatures (15–25 °C) (Climate Data 2022, <https://climate-data.org>). The mean annual rainfall is ~980 mm, of which more than 80% precipitates during the monsoon season from southwest monsoon (Singh et al. 2010). The area is mainly dominated by fragmented forests of dry deciduous vegetation (Champion and Seth 1968; Sagar and Singh 1999, 2003). The soil varies from loamy sand to clay in texture with nutrient-deficient Ultisols. Variation in soil color is from reddish to dark gray (Singh et al. 1989). The dominant tree species in the area are *Adina cordifolia* (Roxb.) Brandis, *Buchania lanzan* Spreng., *Boswellia serrata* Roxb., *Hardwickia binata* Roxb., *Lannea coromandelica* (Houtt.) Merr., *Lagerstroemia parviflora* Roxb., *Madhuca longifolia* (L.) J.F. Macbr., *Senegalia catechu* (L.f.) P.J.H. Hurter and Mabb., *Shorea robusta* C.F. Gaertn., *Tectona grandis* L.f., and *Terminalia anogeissiana* Gere and Boatwr (Sagar and Singh 1999, 2003, 2006; Sharma and Raghubanshi 2009).

Study species

Hyptis suaveolens (L.) Poit. (Lamiaceae) is a dominant invasive plant in tropical and subtropical regions worldwide. It is an annual native species of tropical America. It is a branching herb that grows up to 2–2.5 m in height. Leaves are simple ovate, opposite, and decussate with 2–4 cm long petioles. It bears small bluish-purple, 2–5 flowered raceme inflorescences on leaf axils. The flowers are pollinated by a huge number of pollinators, leading to an ample amount of polymorphic black-coloured fruits (~3000 seeds m⁻²) (Sharma and Raghubanshi 2009; Shah et al. 2024). It can grow well

under a wide range of environmental conditions due to its high plastic responses (CABI 2024; Shah et al. 2024).

Sampling strategy

The field study was carried out in the monospecific thickets of *H. suaveolens* during the peak growing season of the years 2021 and 2022. The peak growing season for herbaceous species lies between August and November, before the onset of the dry period (December–June) in dry deciduous regions of the Vindhyan highlands (Kushwaha et al. 2011). Across the study area, distinct populations were identified by reconnaissance through the *H. suaveolens*-infested area to identify groups of plant individuals isolated by at least 100 m from any other *H. suaveolens* populations. Among these isolated monospecific populations, 100 quadrats (5×5 m²) were randomly laid down to estimate *H. suaveolens* population density. The number of *H. suaveolens* plants in each quadrat was recorded to estimate the population density of each quadrat. Based on the population density, sampling quadrats/patches were divided into low-, medium-, and high-density population groups. It was explicitly made sure that each studied quadrat should encompass a spatially segregated *H. suaveolens* monospecific patch with clear boundaries (having no or very few *H. suaveolens* individuals around the sides of the quadrat) (hereinafter, quadrat and patch will be used interchangeably and will be referred to collectively as quadrat/patch).

For each quadrat, plant performance traits were studied at two scales—fine scale and coarse scale. Two sets of performance traits, namely plant traits (PITs) and patch traits (PaTs), were estimated at fine scale and coarse scale, respectively (Table 1). Further, PITs and PaTs were correlated to understand the population dynamics of *H. suaveolens* across varying population densities. The study was designed to understand the effects of population density on the plant trait performance that is manifested through species-specific traits, i.e., plant fitness traits—vegetative growth and reproductive output (Goyal et al. 2018; Shah et al. 2024; also see Shah 2024).

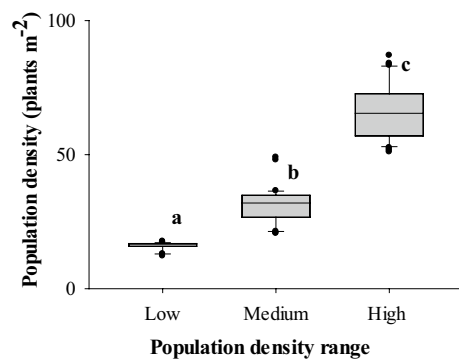
Plant traits (PITs)

Within each of the quadrats/patches, 10 healthy plant individuals were harvested by clipping the plant shoots just above the soil surface and assessed for estimation of PITs—vegetative traits and reproductive traits (Singh et al. 2011; Goyal et al. 2018; Shah et al. 2024). Vegetative growth was assessed through maximum vertical extent or plant height (cm), maximum horizontal expanse or number of secondary stems per plant per plant, and plant dry biomass (aboveground dry biomass per plant) (mg) of the selected plant individuals (Kardol et al. 2010). The number of seeds per plant, seed size (mm), and seed mass

Table 1 The values of plant traits (PITs) and patch traits (PaTs) of *Hyptis suaveolens* (L.) Poit. individuals across three population densities at fine scale and coarse scale, respectively

Parameters	Mean values			F value; <i>df</i> _{2,97}	p values
	Population density range				
	Low	Medium	High		
Fine scale					
Plant traits (PITs)					
Vegetative traits					
Plant height (cm)	116.51 ^a (13.42)	187.99 ^b (14.13)	156.78 ^c (15.33)	71.72	0.000 [*]
Plant biomass (g)	08.08 ^a (1.36)	13.81 ^b (2.27)	11.79 ^c (2.44)	68.13	0.000 [*]
Number of secondary stems per plant per plant	16.86 ^a (2.69)	10.16 ^b (1.33)	6.85 ^c (1.54)	88.30	0.000 [*]
Reproductive traits					
Number of seeds per plant	117.32 ^a (16.82)	60.43 ^b (15.65)	155.04 ^c (17.14)	53.06	0.000 [*]
Seed size (mm)	03.89 ^a (0.48)	03.53 ^a (0.37)	03.33 ^a (0.57)	17.56	0.968 ^{NS}
Seed mass (mg)	03.60 ^a (0.98)	03.57 ^a (0.67)	03.54 ^b (0.57)	.033	0.000 [*]
Coarse scale					
Patch traits (PaTs)					
Population density (plants m ⁻²)	15.98 ^a (2.24)	31.43 ^b (4.12)	65.76 ^c (6.82)	436.99	0.000 [*]
Plant biomass per patch (g)	1620.33 ^a (272.43)	5168.61 ^b (501.23)	5009.28 ^b (321.00)	82.56	0.000 [*]
Number of seeds per patch	23,513.60 ^a (2439.57)	23,691.38 ^a (3924.49)	66,978.14 ^b (8219.22)	52.45	0.000 [*]

Values in parentheses are $\pm$ SE. p values marked with * are significantly different at $p < 0.05$ and those marked with NS are not significantly different. Numerical values marked with different letters a, b, and c are significantly different from each other according to Tukey's HSD test at $p < 0.05$

**Fig. 2** Population density of *Hyptis suaveolens* (L.) Poit. individuals studied across three different population density ranges (low, medium, and high). Letters a, b, and c show significant differences from each other according to Tukey's HSD test at $p < 0.05$

(mg) were quantified to understand reproductive trait performance (reproductive output).

Patch traits (PaTs)

In each quadrat/patch, *H. suaveolens* population density (plants m⁻²) was estimated (Fig. 2). Population density was categorized into low-density (average number of plants, ~200), medium-density (average number of plants, ~374), and high-density (average number of plants, ~427) groups. Using the plant trait values,

PaTs—plant biomass per patch (g) and the number of seeds per patch—were estimated. Plant biomass per patch was calculated as multiplying plant dry biomass (that was calculated for the PITs) by the number of plant individuals per patch. Similarly, the number of seeds per patch was calculated as multiplying the number of seeds per plant (that was calculated for the PITs) by the number of plant individuals per patch.

Plasticity response index

The values of PITs and PaTs were used to determine the plasticity response index (PI). PI values were calculated between the plant performance trait values of plant individuals inhabiting low and medium densities and between the plant performance trait values of plant individuals inhabiting medium and high densities, respectively. For a comparative assessment, these values are expressed as a surrogate measure for estimating the plastic responses/trait modulations of *H. suaveolens* individuals transitioning between the low-to-medium (LTM) density quadrats/patches and between medium-to-high (MTH) quadrats/patches, respectively (refer to the sampling strategy of the Material and Methods section) (Table 2). PI values range from 0 (no plastic response) to 1 (maximal plastic response) for all the studied performance traits. PI values were calculated as the difference between maximum and minimum mean values divided

Table 2 Plastic response index (PI) values of plant traits (PITs) and patch traits (PaTs) of *Hyptis suaveolens* (L.) Poit.

	Plastic response index (PI)	
	LTM	MTH
Fine scale		
Plant traits (PITs)		
Vegetative traits		
Plant height	0.38 ^m	0.17 ^l
Plant biomass	0.41 ^m	0.15 ^l
Number of secondary stems per plant per plant	0.40 ^m	0.34 ^m
Reproductive traits		
Number of seeds per plant	0.48 ^m	0.67 ^h
Seed mass	0.01 ^l	0.01 ^l
Seed size	0.09 ^l	0.06 ^l
Coarse scale		
Patch traits (PaTs)		
Plant biomass per patch	0.69 ^h	0.03 ^l
Number of seeds per patch	0.02 ^l	0.65 ^h

^l low, ^m moderate, and ^h high represent PI values corresponding to different plant trait (PITs and PaTs) that were calculated for low-to-medium (LTM) density quadrats/patches and for medium-to-high (MTH) density quadrats/patches, respectively

by maximum mean values of PITs and PaTs. Moreover, PI values were divided into three range categories exhibiting *low* (PI 0.00–0.33), *moderate* (PI 0.34–0.66), and *high* (PI 0.67–1.00) phenotypic plastic response (Valladares et al. 2005; Gratani et al. 2014; Shah et al. 2024).

Statistical analyses

Principal Component Analysis (PCA) was performed with the help of BioDiversity Professional software (McAleece 1997) to understand the differences in plant traits (PITs) and patch traits (PaTs) due to variable population densities. Pearson correlation was performed to identify the relationship among and between the PITs and PaTs. The effect of population density on the studied PITs and PaTs was analyzed with a one-way ANOVA. Tukey's HSD test was conducted to identify the significant differences among the different population densities. Statistical analyses were performed using SPSS 16.0 (SPSS Inc. 2007, Chicago, USA).

Results

Results revealed that the studied monospecific thickets of *Hyptis suaveolens* exhibited variable population densities: low-density (number of quadrats/patches: 34; average density: 15.98 plants m⁻²), medium-density (number of quadrats/patches: 35; average density: 31.43 plants m⁻²), and high-density (number of quadrats/patches: 31; average density: 65.76 plants m⁻²) in the study area (Fig. 2).

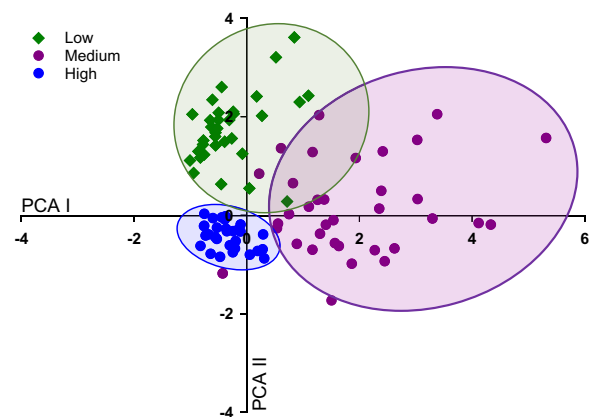
**Fig. 3** Principal Component Analysis (PCA) based on plant traits (PITs) and patch traits (PaTs) of *Hyptis suaveolens* (L.) Poit. across varied population densities (low, medium, and high)

Figure 3 outlines the results of PCA using the two primary component axes, i.e., PCA I and PCA II. PCA axis I accounts for 60% variability, and PCA II accounts for 25% variability. PCA showed that the PITs and PaTs varied across the three population densities. Moreover, PCA revealed that the performance trait values of PITs and PaTs of *H. suaveolens* cluster into three distinct groups, i.e., individuals inhabiting three population densities: low (green cluster), medium (blue cluster), and high (purple cluster). The summary statistics for PITs and PaTs of the plant individuals inhabiting three population densities are compiled in Table 1 and discussed further.

Plant traits (PITs)

Plant growth performance traits (plant height, plant biomass, and number of secondary stems per plant) and reproductive output (only number of seeds) were significantly different at variable population densities (Table 1). Seed size was found to be not significantly different across the three population densities. Interestingly, seed mass was significantly different only between low- and high-density and between medium- and high-density while it showed no significant differences between low- and medium-density. The average plant height and average plant biomass of plant individuals inhabiting all the studied quadrats/patches ranged from 116.51 to 187.99 cm and 8.08 to 13.81 g, respectively. Plant individuals in medium-density showed maximum height (vertical expanse of a plant), whereas individuals in low-density exhibited minimum height. However, an average number of secondary stems per plant (horizontal expanse of a plant) ranged from 6.85 to 16.86, with the lowest in the high-density and highest in the low-density. Plants inhabiting medium-density populations

produced high biomass amongst all three population densities (Table 1).

Plants growing in high-density and medium-density showed the highest ($n=155$) and lowest ($n=60$) seed production, respectively. While comparing reproductive output between low- and medium-density populations, individuals growing in low-density populations were producing more seeds than medium-density populations. Moreover, plants inhabiting low-density populations produced the heaviest (3.60 mg) and largest seeds (3.89 mm) than plants growing in medium- and high-density populations (Table 1).

Patch traits (PaTs)

The three studied population densities, i.e., low, medium, and high, were significantly different from each other (Table 1). Plant biomass per patch was found to be lower

for low-density populations than medium- and high-densities, and it showed a non-significant difference between medium and high densities. The number of seeds per patch was significantly higher for high-density populations than for small- and medium-density populations. Moreover, average reproductive output per patch was found to be similar in low- and medium-density (Table 1). Plant density showed comparatively significant and positive relations with PaTs, e.g., plant biomass per patch and number of seeds per patch, as compared to PITs, e.g., plant biomass per plant and number of seeds per plant (Fig. 4a–d).

The studied PITs and PaTs were correlated to analyze the interrelations (Table 3). PITs such as plant height, plant biomass, and number of seeds per plant showed significant and positive relations with population density. Additionally, population density had significant negative

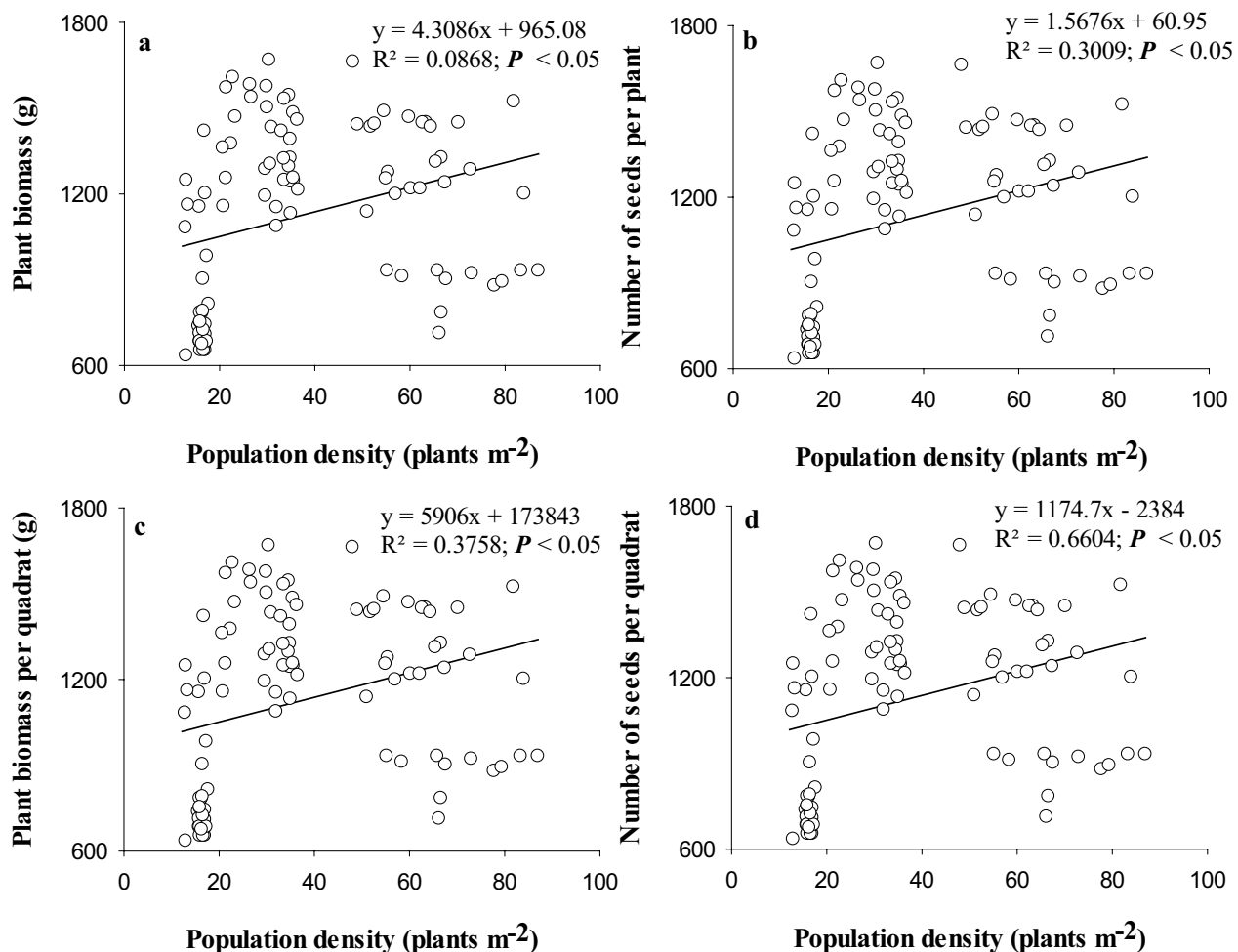


Fig. 4 Scatter plots showing relations between population density and plant traits (PITs), i.e., **a** plant biomass and population density and **b** number of seeds per plant and population density; and relations between population density and patch traits (PaTs), i.e., **c** plant biomass per quadrat/patch and population density and **d** number of seeds per quadrat/patch and population density of *Hyptis suaveolens* (L.) Poit. populations showing variable densities (low, medium, and high)

relations with a number of secondary stems per plant and seed mass, while seed size showed a non-significant relation with population density. Plant height showed significant and positive and significant and negative relations with plant biomass and number of seeds per plant, respectively. Plant biomass showed significant and negative relations with the number of seeds per plant and seed mass. For PaTs, plant biomass per patch showed significant and positive relations with population density and plant height, while it was significantly and negatively related to the number of secondary stems per plant and seed mass (Table 3). The number of seeds per patch exhibited significant and positive relations with population density and the number of seeds per patch, whereas it was significantly and negatively related to the number of secondary stems per plant and seed mass.

Plasticity response index

Plant individuals showed variable trait modulations in PITs and PaTs in response to different population densities (Table 2). Among the PITs and PaTs, the number of seeds per plant showed the highest PI values for MTH, while seed mass showed the lowest PI values for both LTM and MTH. Comparative assessment of plastic responses reflected that PITs showed low, medium, and high plastic responses, whereas PaTs exhibited low and high plastic responses. Vegetative PITs, plant height, and plant biomass showed *medium* and *low* plastic responses for the LTM and MTH, respectively. The plastic responses for reproductive PITs—number of seeds—exhibited *medium* and *high* plastic responses for the LTM and MTH, respectively. Whereas both seed size and seed mass showed low plastic responses for the LTM and MTH. For PaTs, plant biomass per patch showed *high* and *low* plastic response for LTM and MTH, respectively,

while the number of seeds per patch followed the inverse trend.

Discussion

Plant traits (PITs)

The findings impressed upon the existence of the component Allee effect in a dominant plant invader, *Hyptis suaveolens*, where the number of seeds per plant, as an important component of species fitness, was lower for low- and medium-density populations and higher for high-density populations (i.e., positive density-dependence in reproductive output). Numerous other studies have also reported low reproductive output of plant invaders exhibiting sparse and low-density populations (van Kleunen and Johnson 2007; Monty and Mahy 2010; Lachmuth et al. 2018; Edgar et al. 2022). It can be argued that a decrease in seed production at low density does not always imply that the invasive population exhibits Allee effects. In order to prove the existence of Allee effects, the reported occurrence of ‘a decrease in seed production at low density’ should be complemented by taking into consideration the low-density effects not only on reproduction but also on vegetative growth and proliferation (i.e., the reported occurrence of short-statured and low biomass-producing plants in low-density populations in comparison to high-density populations). As Allee effects do not cause only a reduction in species fitness for a subset of individuals (those of reproductive size), they cause a reduction in overall species fitness (or components of species fitness) across various life-history traits (Courchamp et al. 2008; Weber and Kolb 2013; Kanarek et al. 2015; Nagel et al. 2021).

Interestingly, the observed comparatively high reproductive output in low-density populations compared

Table 3 Correlation matrix among the plant traits (PITs) and patch traits (PaTs) of *Hyptis suaveolens* (L.) Poit.

	PD	PH	PB	NS	SN	SS	SM	PBP	NSP
PD	1								
PH	0.327**	1							
PB	0.295**	0.622**	1						
NS	− 0.677**	− 0.385**	− 0.495**	1					
SN	0.411**	− 0.245*	− 0.237*	− 0.059	1				
SS	− 0.047	− 0.067	− 0.043	− 0.083	0.093	1			
SM	− 0.442	− 0.223*	− 0.364**	0.448**	− 0.047	0.315**	1		
PBP	0.613**	0.585**	0.768**	− 0.549**	0.003	− 0.035	− 0.406**	1	
NSP	0.738**	0.115	0.125	− 0.341**	0.810**	− 0.007	− 0.295**	0.512**	1

PD Population density (plants m^{−2}), PH Plant height (cm), PB Plant biomass (g), NS Number of secondary stems per plant per plant, SN Number of seeds per plant, SS Seed size (mm), SM Seed mass (mg), PBP Plant biomass per patch (g), NSP Number of seeds per patch

*Correlations significant at level 0.05

**Correlations significant at level 0.01

to medium-density populations was probably due to the production of a higher number of secondary stems per plant in individuals of low-density populations than in medium- and high-density populations (i.e., negative density-dependence in vegetative growth). *H. suaveolens* bears seeds in the axillary positions of its primary and secondary stems, so the production of a high number of secondary stems per plant facilitates high reproductive output. Production of secondary stems in a plant measures its horizontal expanse and acts as a survival strategy employed by plant individuals in response to unfavorable conditions (Feldman and Morris 2011). In all likelihood, plant individuals allocated more resources towards the production of a high number of secondary stems per plant and hence a high number of seeds in low-density populations. Under such a scenario, less resource allocation towards the vertical expanse of a plant (plant height) and biomass accumulation gave rise to short-statured individuals in low-density populations, while plants growing in medium- and high-densities were long-statured (i.e., positive density-dependence in vegetative growth).

Additionally, the production of large-size and heavy-weight seeds and small-size and light-weight seeds at low- and high-density, respectively, may be one of the significant trait modulations/plastic responses of *H. suaveolens* (negative density dependence in reproductive output). Feldman and Morris (2011) studied the combined effects of positive density-dependence in reproductive output and negative density-dependence in vegetative growth in *Piriqueta cistoides* subsp. *caroliniana* (Walter) Arbo. Similarly, *H. suaveolens* exhibited a combination of both negative and positive density-dependence in vegetative growth as well as in reproductive output. It is probable that as the population grows to medium-density from the low-density, an increase in vegetative trait performance (plant height and biomass) outweighed the negative effects of declining reproductive output (number of seeds). This occurs as increasing population density was significantly and positively related to vegetative growth (number of secondary branches), while it has no significant relation to reproductive output (number of seeds). The compensatory interactions among vegetative growth and reproductive output enable *H. suaveolens* individuals to overcome the deleterious effects of Allee effects dynamics in low-density populations.

Patch traits (PaTs)

Primary patches are the low-density monospecific thickets that were established early in the species establishment process. These primary patches grow to a larger size and typically form satellite patches in adjacent areas

at later stages of a successful invasion (Campbell et al. 2017; Baer and Maron 2018; Eppinga et al. 2021). Successful patch transitions are determined by the invader's varied trait performance and plastic responses. In the present study, *H. suaveolens* individuals exhibited a *medium* plastic response in vegetative trait performance for LTM while a *low* plastic response for MTH (except number of secondary stems per plant). However, the number of seeds per plant showed a *medium* plastic response for LTM and a *high* plastic response for MTH. It is noteworthy that for vegetative traits, *medium* plastic responses at fine scale (plant traits) gave rise to *high* plastic responses at coarse scale (patch traits) for LTM. The peculiar density-dependent behavior of *H. suaveolens* individuals growing in variable population density can be explained by using the phrase, 'Wisdom of the crowd'. Overall, it is suggested that in *H. suaveolens* populations, fine scale (plant traits) modulations get positively translated into coarse scale (patch traits) modulations. It is anticipated that expanding populations of *H. suaveolens* exert invasion pressure through plant biomass accumulation at medium-density quadrats/patches and in the form of reproductive output at high-density quadrats/patches in habitats.

Heavy-weight and large-sized seeds produced by low-density populations of *H. suaveolens* facilitate a high probability of 'on-site' seed germination and seedling recruitment for a low-density population, thus leading to a local establishment. Additionally, large-size seeds could also enhance a seedling's competitiveness and tolerance to a wide range of environmental conditions (Daws et al. 2007; Ambika et al. 2014; Khatri et al. 2023, 2024a). In a larger time frame, these established seedlings would give rise to self-sustaining local populations showing positive population growth, thus facilitating the transitions of low-density quadrats/patches to medium-density quadrats/patches. Once the population reaches medium-density, *H. suaveolens* exhibits rapid biomass production, thus leading to a masking effect on other resident plant species of the recipient ecosystem. The rapid biomass production gives rise to denser populations and facilitates the transition of medium-density quadrats/patches to high-density quadrats/patches. Such rapid biomass production at medium-density coupled with high reproductive output at high-density facilitates *H. suaveolens* expansion in the dry deciduous forest of Vindhyan highlands, India. Moreover, for plant individuals growing in high-density patches, production of light-weight and small-size seeds ensures the high probability of 'off-site' seed germination and seedling recruitment, thus leading to long-distance regional expansion of *H. suaveolens* to adjacent areas. Owing to this peculiar strategy, the plant invader is able to perform at its best to maintain a

self-sustaining population at low-density and lead population expansion at high-density.

Associative effects of both PITs and PaTs modulations

The striking difference in plastic responses among plant traits performance corresponding to PITs and PaTs of plant populations inhabiting small-, medium-, and high-density quadrats/patches advertises for *H. suaveolens* trait modulation ability operating at two scales. At the fine scale (plant traits), plastic responses (intrinsic trait modulations) potentially increase the ecological breadth of invasive species, thus facilitating the enhanced expression of advantageous plant traits in a broad range of environmental settings (Palacio-López and Gianoli 2011; Pérez-Ramos et al. 2019; Khatri et al. 2023, 2024b). At coarse scale (patch traits), extrinsic trait modulations enable *H. suaveolens* to exhibit compensatory interactions among two different plant traits or two different components of species fitness (i.e., reduced expression of one particular plant trait or component of species fitness in response to enhanced expression of another plant trait or component of species fitness). The extrinsic trait modulations can be termed as *elastic responses*. In addition to the plastic responses of a species, it is proposed that the term *elastic responses* can be used to explain the peculiar density-dependent behavior exhibited by *H. suaveolens*. At coarse scale (patch traits), the trait modulations operate elastically rather than plastically. When subjected to a spectrum of population densities (low-to-medium-to-high), *elastic responses* enable the trade-off between two plant traits or components of species fitness in response to the increasing population density, where an enhanced response of one trait is correlated with a reduced response in another (or vice versa).

Evidently, as an important example from the study, to compensate for the *low* plastic response of reproductive trait (number of seeds per patch), vegetative plant trait (plant biomass per patch) showed a *high* plastic response for LTM. Interestingly, an inverse trend was observed for MTH—this time for compensating the *low* plastic response of vegetative trait (plant biomass per patch), reproductive plant trait (number of seeds per patch) exhibited a *high* plastic response. Invasive spread outside of the introduction regions often relies on the reproductive output of invaders (Goyal et al. 2018; Daly et al. 2023; Khatri et al. 2023; Shah et al. 2024); thus, a high plastic response for the production of light-weight and small-sized seeds coupled with a high number of seeds at coarse scale provides fitness advantages. It is anticipated that these compensatory responses arising due to the greater plastic responses of *H. suaveolens* might protect the invading populations from Allee effects and thus play a crucial role in

its invasion success in invaded habitats. Figure 5 shows the temporal fluctuations in population density (i.e., lag phase) as well as the spatial dimension of the population expansion (i.e., local spread) shown by *H. suaveolens* populations exhibiting the Allee effects dynamics during their local spread and regional expansion.

It is noteworthy that the occurrence of the component Allee effect could explain the 'lag phase,' i.e., the slow rate of expansion at low density exhibited by the invading populations of *H. suaveolens* in the dry deciduous forest of the Vindhyan highlands. Lag phase was also reported in other invasive species, such as the example of *Pinus strobus* L. in central Europe, which was not considered to be an invader until 250 years after the first reported introduction (Schmitt 1972). *Vachellia nilotica* (L.) P.J.H. Hurter & Mabb. became an obnoxious invasive species in Australia between the 1890s and 1950s after a prolonged lag phase (Mack 1981). Similarly, *Bassia scoparia* L. was also introduced in Wyoming in the 1880s and not reported to invade other states of the USA until the 1950s (Friesen et al. 2009). It is anticipated that in the case of *H. suaveolens*, owing to the Allee effects dynamics, the observed component Allee effect at the fine scale plays an important role in the occurrence of the lag phase at the coarse scale.

It is interesting to note that although Allee effects, owing to lag phase, potentially slow the rate of spread of an invasive species, if an invading population overcomes the deleterious impact of the Allee effects, then the Allee effects dynamics are no longer the limiting factor for its proliferation and spread (Groom 1998; Taylor and Hasting 2005; Feldman and Morris 2011; Hui and Richardson 2017; Gioria et al. 2023). Thus, allowing the suboptimal population growth and local spread at low-density with the rapid increase in population growth at medium-density and regional expansion at high-densities. The present study suggests that combined effects of positive density-dependence and negative density-dependence in vegetative growth and reproductive output are driving the population dynamics of *H. suaveolens* in dry deciduous regions of the Vindhyan highlands. Thus, accounting for Allee effects dynamics in the non-native species spread and expansion could augment our ability to better generate the management strategies for the most alarming fronts for biological invasions and mitigate the ongoing and/or future non-native colonization incidents.

Conclusion

H. suaveolens populations undergoing Allee effects show reduced vegetative growth at low-density. As population density increases up to medium-density,

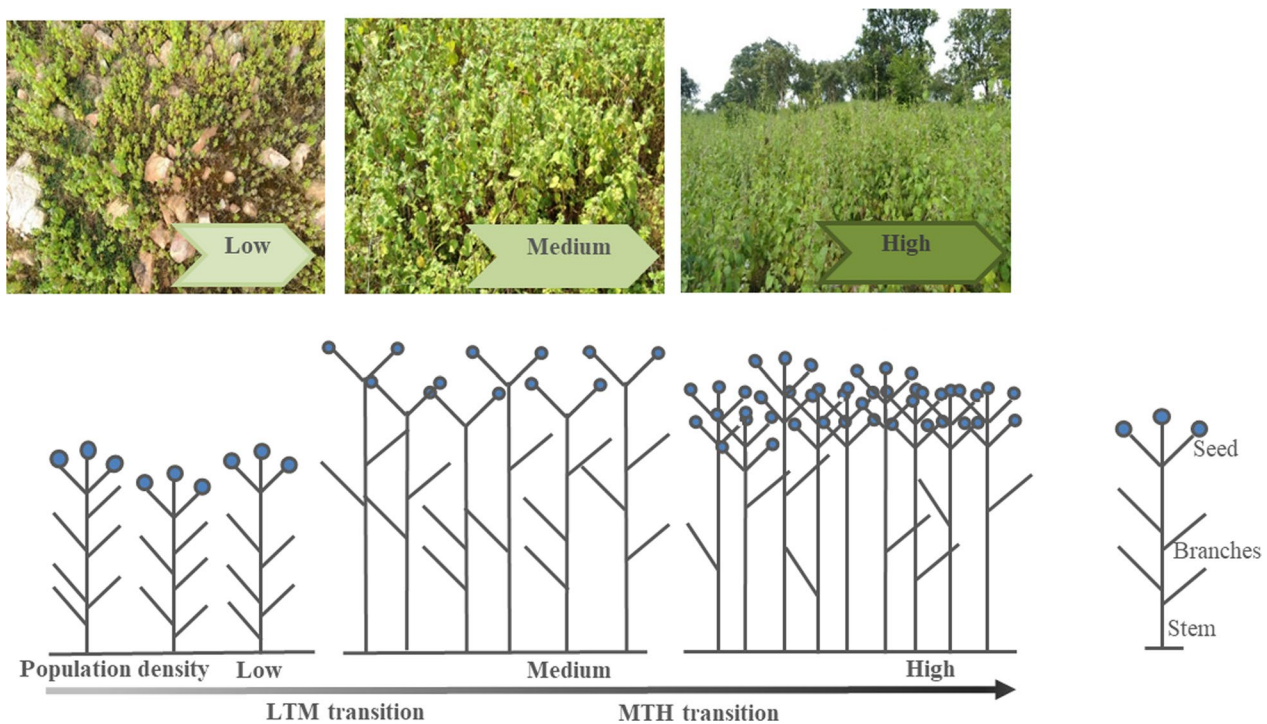


Fig. 5 Temporal fluctuations in population density (i.e., lag phase) as well as the spatial dimension of the population expansion (i.e., local and regional spread) shown by *Hyptis suaveolens* (L.) Poit. populations during the transition from low-to-medium (LTM) and medium-to-high (MTH) population density quadrats/patches

expansion occurs more rapidly and gives rise to denser populations (typified by significantly higher vegetative growth but lower reproductive output). Medium-density populations exert high biomass-associated negative impacts on recipient habitats, and if left unchecked, they would grow into high-density populations with high reproductive output (typified by significantly higher seed production and a lower number of secondary branches). It is anticipated that through compensatory interactions, *H. suaveolens* overcomes the deleterious impacts of the Allee effects. Considering that invasive populations of *H. suaveolens* exhibit rapid biomass generation at medium-density and high seed output at high-density in recipient habitats. The findings suggest that areas showing low-density populations should be considered as high-priority areas for developing efficient and cost-effective management strategies. Additionally, the study suggests that physical removal, a most common management strategy, of plants in medium- and high-density areas would provide varied advantages in the invaded habitats. Removing plants in medium-density showing high biomass generation may delay 'on-site' seedling establishment, thus allowing other native plants to grow in the available space previously occupied by the *H. suaveolens* individuals. Physical removal of plant individuals in

high-density exhibiting high seed output might be beneficial for keeping a check on 'off-site' seedling establishment/proliferation, as the number of seeds supplied for long-distance/regional expansion would be significantly reduced. Incorporation of Allee effects dynamics in invasion studies is critical for predicting the population growth and rate of spread of non-native species in local/regional recipient habitats. Thus, the study augments the identification of high-priority areas for strategizing management of fast-spreading plant invaders.

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Author contributions

Conceptualization: KS and GPS; data collection: KS; data analysis: KS and GPS; writing-original draft preparation: KS and GPS; writing-review and editing: KS and GPS. All authors have read and agreed to the published version of the manuscript.

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Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent for publication

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Competing interests

The authors declare that they have no competing interests.

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